

Article



Descriptions of three new species of *Melanochromis* (Teleostei: Cichlidae) and a redescription of *M. vermivorus*

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Abstract

The Lake Malaŵi genus *Melanochromis* included five species at its inception and was originally distinguished from *Pseudotropheus* on the basis of morphology including the arrangement of pharyngeal teeth. The diagnosis has been extended twice, first to include all elongate mbuna that possess horizontal stripes and U-shaped tooth bands and later to exclude mbuna that do not exhibit a sex-related reversal in their color pattern. We have further refined the diagnosis of the genus on the basis of the melanin pattern, resolved a longstanding dispute regarding the validity of *M. heterochromis*, re-evaluated the status of *M. vermivorus*, synonymized *M. mellitus* Johnson 1976 with *M. melanopterus* Trewavas 1935, moved *M. benetos* Bowers and Stauffer 1977 to *Pseudotropheus*, and described *M. kaskazini*, *M. wochepa*, and *M. mossambiquensis* from the eastern shore of the lake. *Melanochromis* is still paraphyletic as two species, *M. joanjohnsonae* Johnson 1974 and *M. labrosus* Trewavas 1935, are not congruent with the rest of the group, but, currently, a better alternative for these two could not be found.

Key words: Malawi, cichlid, mbuna, melanin pattern

Introduction

The small, rock-dwelling haplochromine cichlid fishes in Lake Malaŵi, Africa, are commonly referred to as mbuna. The genus Melanochromis Trewavas 1935—one of the dozen genera currently recognized within the mbuna—was originally distinguished from *Pseudotropheus* on the basis of the less numerous and less densely crowded pharyngeal teeth with those of the middle series becoming a little larger posteriorly in Melanochromis. Based on these characters, five new species were initially included in the genus: Melanochromis melanopterus, M. vermivorus, M. brevis, M. perspicax, and M. labrosus. Johnson (1975) proposed to classify the species in the genera Melanochromis and Pseudotropheus on the basis of their color pattern and suggested to include P. auratus, P. johannii, and P. fuscus in Melanochromis and to transfer M. brevis to Pseudotropheus. On the basic of the morphology of the lower pharyngeal jaw in P. johannii and in P. auratus, Burgess (1976) also placed these two species in Melanochromis. A few years later, Johnson (1978) reconsidered some of his propositions and returned M. brevis to Melanochromis and P. fuscus to Pseudotropheus. Two of the species originally included in Melanochromis, M. labrosus and M. perspicax, lack horizontal stripes; the latter has, on the basis of its color pattern, tentatively been placed in Pseudotropheus by Loiselle (1979) and by Ribbink et al. (1983). The generic placement of M. labrosus has always been disputed, and at some point it was questioned whether it belongs to any of the genera commonly referred to as mbuna (Burgess 1976; Loiselle 1978; Genner & Turner 2005). It currently resides in Melanochromis.

Trewavas (1984) extended her initial diagnosis of Melanochromis to include, among others, color pattern

characteristics as follows: members of the genus are characterized by a pattern of horizontal stripes comprising pale bands, often iridescent, on a black or very dark background. Not until Trewavas's extended diagnosis were the earlier proposed definitions, based on color pattern, generally accepted. In 1982, Ribbink and Lewis described *Melanochromis crabro* on the basis of the morphology of its lower pharyngeal jaw, but Trewavas (1984) transferred it to *Pseudotropheus* on the basis of its color pattern, which consists of vertical bars.

A relatively large number of species have since been added to Melanochromis. Eccles (1973) described M. simulans while Burgess and Axelrod (1976) added M. parallelus. The latter species was regarded a junior synonym of M. chipokae by Schraml (1998). Johnson (1974, 1975a, b, 1985) added a number of species to Melanochromis: M. chipokae, M. loriae, M. interruptus, M. mellitus, M. joanjohnsonae (originally described as a member of Labidochromis but placed in Melanochromis by Lewis in 1980), and M. robustus. Melanochromis loriae Johnson 1975 was regarded as a junior synonym of M. chipokae (Konings 2001), and M. mellitus Johnson 1976 has previously been considered a junior synonym of M. vermivorus (Schraml 1998; Konings 2001). M. mellitus appears herein to be congruent with M. melanopterus, which makes it a junior synonym. Bowers and Stauffer (1993) described M. heterochromis, and in 1997 the same authors added M. dialeptos, M. cyaneorhabdos, M. perileucos, M. baliodigma, M. xanthodigma, M. lepidiadaptes, M. benetos, and M. elastodema. The latter species has subsequently been regarded as a junior synonym of M. interruptus Johnson (Schraml 1998; Konings 2001), and Konings (2001) regarded M. xanthodigma conspecific with M. baliodigma and M. benetos a junior synonym of M. robustus Johnson. Tawil (2002) argued that there are at least two fundamentally different color patterns among the present members of *Melanochromis* and that M. johannii, M. interruptus, M. perileucos, and M. cyaneorhabdos are therefore probably not closely related to M. melanopterus. He redefined the diagnosis and suggested moving these four species to Pseudotropheus.

One of the contentions regarding the identification of species of *Melanochromis* is that involving *M. vermivorus*. *Melanochromis vermivorus* had not been recognized in the field and mistaken as a variant of *M. melanopterus* (Ribbink *et al.* 1983), while *M. heterochromis* had been seen as a possible geographical variant of *M. vermivorus* (Konings 1995; Schraml 1998). Previous attempts to collect *M. vermivorus* at its type locality (Nkudzi, Malaŵi) were unsuccessful because of the confusion of that species with *M. melanopterus* and because of the mistaken perception of how *M. vermivorus* would look like alive, due to an earlier misidentification of the species later described as *M. heterochromis*. We recently collected *M. vermivorus* from the type locality and recognized behavioral differences when we compared it to *M. melanopterus* or *M. heterochromis*. We therefore chose to further evaluate these three species from the periphery of their respective distributions where that of *M. vermivorus*, which is not sympatric with either *M. melanopterus* or *M. heterochromis*, is about 12 km apart from that of the others. Here we confirm the heterospecificity of these three taxa.

In our continuing attempt to better determine the various assemblages among Lake Malaŵi mbuna, we propose a diagnosis for *Melanochromis*, describe three new species, re-evaluate the status of *M. vermivorus* and *M. mellitus*, and give a nomenclatorial overview of the species that are, or have been, placed in this genus.

Materials and methods

Fishes were collected by the authors in Lake Malaŵi (Fig. 1) by chasing them into a monofilament net while SCUBA diving. Fishes were anesthetized with clove oil, preserved in 10% formalin, and placed in 70% ethanol for permanent storage. All counts and measurements were made on the left side of the fish, with the exception of gill-raker counts. Counts and measurement follow Barel *et al.* (1977) and Stauffer (1991; 1994) with the following exceptions. Head depth was measured from the hyoid symphysis to the top of the (non-expanded) head at a 90° angle to the horizontal body axis (horizontal line drawn through the lower part of lateral line). Body depth was measured from the origin of the fifth dorsal spine to the origin of the pelvic fins. The pre-orbital depth was measured as the length of the intersection of the lachrymal bone with a line

continuing the radius of the orbit and parallel to the snout profile, dissecting the lachrymal bone (Eccles & Trewavas 1989). Institutional abbreviations follow Leviton *et al.* (1985).



FIGURE 1. Map of Lake Malaŵi with localities mentioned in the text.

Pigmentation patterns were recorded in the field, in territorial and non-territorial males, females, and juveniles. The different patterns are variable in all species examined, and in the descriptions such variation is recorded by placing a slash between the two colors between which the specific pattern varies, e.g., blue/white is used to designate that the color ranges from blue to white and includes intermediate shades in certain individuals. The angle of the ethmo-vomerine block was assessed in prepared skulls by measuring the angle between the horizontally-aligned parasphenoid and a line bisecting the vomer (in lateral view) in two equal halves.

Morphometric data were analyzed using sheared principal component analysis (SPCA), with the covariance matrix factored (Humphries *et al.* 1981; Bookstein *et al.* 1985). Meristic data were analyzed with principal component analysis (PCA), with the correlation matrix factored. Differences among species were illustrated by plotting the sheared second principal components of the morphometric data against the first principal components of the meristic data (Stauffer & Hert 1992).

Results

We compared *M. vermivorus*, *M. melanopterus*, and *M. heterochromis* from the periphery of their distribution where they are about 12 km apart, i.e. *M. vermivorus* from Nkhudzi (Fig. 2a) and *M. heterochromis* (Fig. 2b) and *M. melanopterus* (Fig. 2c) from Thumbi East Island. The minimum polygon clusters formed by plotting the PC1 of the meristic data against the SPC2 of the morphometric data for the three taxa (Fig. 3) were significantly different (P<0.05, MANOVA). Variables that had the highest loading on the second principal components of the morphometric data were cheek depth (0.24), post dorsal to ventral caudal (0.23), and snout to pelvic fin (0.20); while those with the highest loadings on the principal components of the meristic data were number of gill rakers on outer ceratobranchial (0.23), tooth rows lower jaw (0.23), and pectoral rays (0.23).

The morphological difference between *M. vermivorus* and *M. heterochromis* is best expressed in the length of the lower jaw in relation to head length. In *M. vermivorus* (Nkhudzi; n=18 and Boadzulu Island; n=22), the lower jaw length ranged between 32.0–41.5 % HL, and in *M. heterochromis* (Thumbi East Island; n=20) the range was 29.3–34.6 % HL. The length of the lower jaw in a part of the type series of *M. vermivorus* (Nkhudzi; n=5) ranged between 34.5 and 36.0 % HL. Bowers and Stauffer (1993) compared *M. heterochromis* (n=184) with all types of *M. vermivorus* (n=20) and found mainly overlapping characters, although the two species segregated totally in a principal component analysis. The relative length of the lower jaw was not included in their study.

Melanochromis vermivorus Trewavas 1935

(Fig. 2a; Table 1)

Melanochromis vermivorus Trewavas 1935:79

Non-type material examined. PSU 4550, 16, 53.0–76.0 mm SL and AMNH 246007, 2, 58.3–73.9 mm SL; Malaŵi: Lake Malaŵi: Nkudzi: 14° 9.772' S, 35° 0.011' E, Stauffer and Konings, 10 Oct. 2004; PSU 4554, 22, 53.0–76.0 mm SL; Malaŵi: Lake Malaŵi: Boadzulu Island: 14° 14.835' S, 35° 8.572' E, Stauffer and Konings, 21 Oct. 2004.

Diagnosis. *Melanochromis vermivorus* is distinguished from its congeners that exhibit the reverse malefemale stripe coloration, except *M. melanopterus*, by the yellow-brown to dark brown ground color (which is cream white to bright yellow in the other species) and from *M. melanopterus* by a larger interorbital width (18.5–25.5 % vs. 16.6–20.6 % HL) and by a deeper head (80.5–99.4 % vs. 68.7–82.0 % HL).

Description. Morphometric ratios and meristic values appear in Table 1. Moderate elongate species (mean BD 32.5% SL) with greatest body depth at about base of fourth dorsal spine. Dorsal body profile gradually curving to caudal peduncle; ventral body profile slightly convex anteriorly and gradually curving upward along base of anal fin. Dorsal head profile straight between snout tip and interorbital, making 40–45° angle with body axis, then rounding to dorsal fin origin; eye (mean 31.6% HL) larger than depth preorbital and positioned in anterior half of head with posterior orbit margin lying on or slightly posterior of vertical median of head. Snout long with isognathous jaws and somewhat thickened lips; teeth on lower jaw in 3–4 rows with outer row bicuspid and inner rows tricuspid. Teeth of lower pharyngeal bone well spaced with a sharp cusp; teeth of posterior row slightly enlarged.

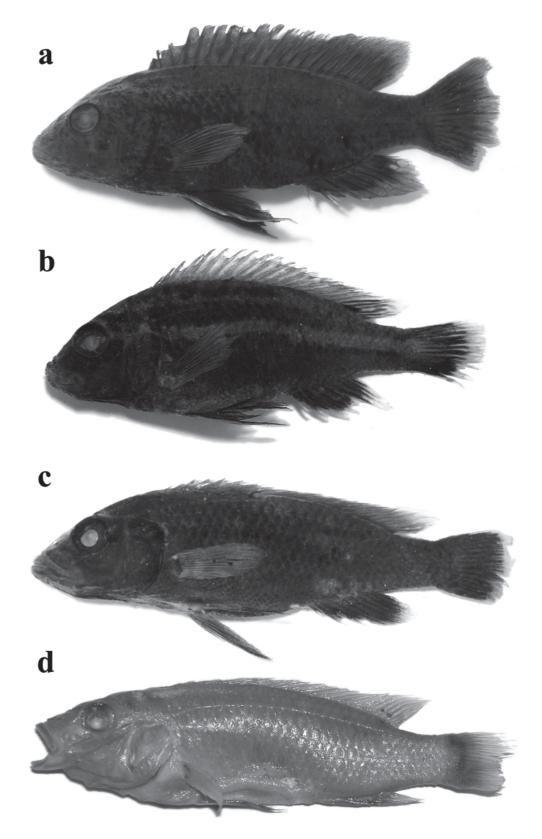


FIGURE 2. Preserved specimens of: a. *Melanochromis vermivorus* from Nkhudzi (PSU 4550, 69.5 mm SL); b. *Melanochromis heterochromis* from Thumbi East Island (PSU 4548, 56.4 mm SL); c. *Melanochromis melanopterus* from Thumbi East Island (PSU 4547, 62.6 mm SL); d. the holotype of *Melanochromis mellitus* from Mumbo Island (AMNH 35387, 79.4 mm SL).

TABLE 1. Morphometric and meristic values of *Melanochromis vermivorus* from Nkhudzi, Malaŵi (n=18) and Boadzulu Island, Malaŵi (n=22).

Melanochromis vermivorus	mean	Nkhudzi range	Boadzulu range
Standard length, mm	65.9	53.0–76.0	56.2-84.0
Head length, mm	22.2	17.8–25.2	18.8–28.1
Percent standard length			
Head length	33.7	32.6–34.8	32.7–36.0
Body depth	32.5	28.6–33.3	30.6–37.3
Snout to dorsal	35.3	33.3–36.9	33.2–38.4
Snout to pelvic	37.8	31.0-39.1	36.3–41.1
Dorsal base length	57.9	54.7–58.0	56.4–61.6
Anterior dorsal to anterior anal	48.2	45.7–48.7	43.3–53.0
Anterior dorsal to posterior anal	61.5	57.8-61.2	59.7–64.9
Posterior dorsal to anterior anal	28.9	27.1–29.4	26.5–31.7
Posterior dorsal to posterior anal	15.3	13.3–16.3	14.5–16.7
Posterior dorsal to ventral caudal	18.8	17.7–20.0	16.9–20.3
Posterior anal to dorsal caudal	20.4	19.1–21.8	19.2–22.2
Anterior dorsal to pelvic-fin origin	32.5	27.2–32.9	30.6–38.5
Posterior dorsal to pelvic-fin origin	55.3	49.4–61.5	48.8–59.1
Caudal peduncle length	13.4	12.7–14.8	11.0–14.6
Least caudal peduncle depth	11.8	10.2-12.2	11.1–13.6
Pectoral fin length	26.0	24.5–31.5	22.1–25.1
Pelvic fin length	25.1	20.4–24.2	19.4–34.9
Percent head length			
Snout length	31.2	28.3-35.1	25.0–35.2
Postorbital head length	44.4	41.9–47.1	41.7–46.6
Horizontal eye diameter	31.6	29.3-34.4	29.5–35.2
Vertical eye diameter	31.7	29.9–35.3	29.7–35.6
Head depth	89.2	80.5-91.5	83.5–99.4
Preorbital depth	20.4	17.8–26.0	13.3–24.7
Cheek depth	27.8	28.2–36.2	20.6–30.3
Lower jaw length	37.0	35.8–41.5	32.0-40.4
Interorbital width	22.1	20.1–23.8	18.5–25.5
Premaxillary length	26.1	22.4–30.0	22.3–29.1
Meristics	mode	range	range
Dorsal fin spines	17	16–18	16–18
Dorsal fin rays	8	7–9	8–9
Anal fin spines	3	3	3
Anal fin rays	7	7–8	7–8
Pectoral fin rays	13	12–14	12–14
Pelvic fin rays	5	5–6	5
Caudal fin rays	17	16–18	16–18
Lateral line scales	32	30–33	31–33

TABLE 1. (continued)

Melanochromis vermivorus	mean	Nkhudzi range	Boadzulu range
Pored scales post lateral line	4	2–5	2–7
Scale row cheek	5	1–5	3–7
Gillrakers 1st ceratobranchial	10	9–10	9–12
Gillrakers 1st epibranchial	3	3	3–4
Teeth outer left lower jaw	12	9–12	8–14
Teeth row upper jaw	3	3–4	2–4
Teeth rows lower jaw	3	3–4	2–4

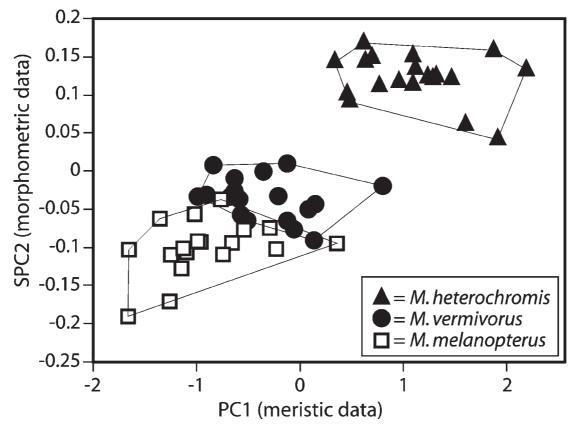


FIGURE 3. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Melanochromis melanopterus* and *M. heterochromis* from Thumbi East Island, and *M. vermivorus* from Nkhudzi.

Dorsal fin with XVI–XVIII (mode XVII) spines and 7–9 (mode 8) soft rays. Anal fin with III spines and 7 or 8 (mode 7) soft rays. First 6–8 dorsal spines gradually increasing in length posteriorly with first spine less than 1/3 length of eighth spine; last 10 spines slightly increasing in length posteriorly with last spine longest; soft dorsal with rounded or subacuminate tip, third or fourth ray longest, not or about reaching base of caudal fin. Anal spines progressively increasing in length posteriorly; fourth or fifth ray longest, reaching to about base of caudal fin, slightly longer than dorsal in males. Caudal fin subtruncate to emarginate. Pelvic fin not reaching anal fin in females; reaching first to second anal spine in males. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base of 10th or 11th dorsal spine.

Flank scales large, ctenoid; abrupt difference to small scales on breast and belly; cheek with 1–7 rows of small scales. Upper branch of lateral line with 19–29 pored scales; lower branch 8–11. Dorsal and anal fins scaleless; small scales over proximal half of caudal fin.

Coloration. Breeding males: head dark blue/black with two, faintly marked light blue interorbital bands;

cheek and gular region blue/black; nape gray/blue. Body dark blue/black with distinct blue midlateral stripe and less distinct blue dorso-lateral stripe; dorsum gray/blue overlain with irregular black markings; caudal peduncle dark blue/black with blue midlateral stripe; belly and breast dark blue/black. Dorsal fin light blue with light blue lappets. Caudal fin dark blue/black membranes and light-blue rays; narrow yellow trailing edge. Anal fin black, with 1–4 orange/yellow ocelli and light blue ventral border. Pelvic fins black with light blue leading margin. Pectoral fins with gray/black rays and clear membranes.

Females: head yellow brown/dark brown with gray/brown gular region. Body yellow brown/dark brown with black midlateral and dorso-lateral stripe. Dorsal, caudal, and anal fins gray/brown with broad yellow/light brown trailing edge. Pelvic fins brown with narrow white/light blue leading margin. Pectoral fins with brown rays and yellow-brown membranes.

Distribution and field observations. *Melanochromis vermivorus* is a rare occurrence in the shallow (< 5 m deep) intermediate habitat at Nkhudzi, Mphande, and Boadzulu islands, but also, even less common, at deeper levels (10–15 m) at Makokola Reef (Fig. 1). Males in breeding coloration are uncommon, and none were seen that defended a breeding territory. The species is attracted to disturbed sediment and appeared to have a mostly opportunistic feeding behavior (stomach analyses were not performed). In this respect, it resembles *M. melanopterus* with which it was never sympatric in our observations and collections. Its distribution lies south of Kanchedza Island in the southeastern arm of the lake, and it has never been found sympatric with *M. heterochromis* either.

Melanochromis kaskazini new species (Figs. 4, 7a; Table 2)

Melanochromis sp. "Northern" Spreinat 1994 Melanochromis sp. 'northern blue' Konings 1995

Holotype. PSU 4546, 121.5 mm SL, male; Tanzania, Lake Malaŵi, Manda, 10° 27.623'S, 34° 34.355' E, Stauffer and Konings, 12 Feb. 2005.

Paratypes. PSU 4545, 11, 69.6–104.2 mm SL, data as for holotype; AMNH 246004, 2, 75.2–99.8 mm SL, same data as for holotype; PSU 4544, 1, 74.0 mm SL, Tanzania, Lake Malaŵi, Lundu: 10° 42.535' S, 34° 39.002' E, Stauffer and Konings, 25 Jan. 2004; PSU 4556, 1, 67.3 mm SL, Tanzania, Lake Malaŵi, Makonde, 9° 56.890' S, 34° 27.301' E, Stauffer and Konings, 8 Feb. 2005; PSU 4543, 5, 53.5–80.8 mm SL, Tanzania, Lake Malaŵi, Ngwazi, 10° 10.485' S, 34° 32.928 ' E, Stauffer and Konings, 10 Feb. 2005.

Diagnosis. *Melanochromis kaskazini* is distinguished from all congeners except *M. lepidiadaptes* by its territorial male coloration, because it exhibits incomplete reverse male-female stripe coloration. Males are cobalt blue and lack any light colored mid-lateral or dorso-lateral stripe. Females are distinguished from other *Melanochromis*, except *M. parallelus*, *M. heterochromis*, *M. lepidiadaptes*, *M. melanopterus*, and *M. simulans*, by a white body color, and differ from these five species by a yellow/orange anal fin, which is white with a black submarginal band in the others. Male *M. kaskazini* with breeding coloration are distinguished from those of *M. lepidiadaptes* by a shallower preorbital (21.9 % vs. 31.8 % HL; ranges: 19.3–26.9 vs. 26.9–35.6), a longer head (34.9 % vs. 31.9 % SL; ranges: 33.6–37.8 vs. 28.4–36.4), a shorter post-orbital head length (42.4 % vs. 47.8 % HL; ranges: 38.4–44.6 vs. 41.8–52.1), and a longer lower jaw (40.3 % vs. 36.8 % HL; ranges: (36.4–44.6 vs. 32.2–40.1).

Description. Morphometric ratios and meristic values appear in Table 2. Spindle-shaped species (mean BD 31.2% SL) with greatest body depth at about base of fourth dorsal spine. Dorsal body profile slightly convex anteriorly and increasingly curving downward along base of soft dorsal fin to caudal peduncle; ventral body profile gradually curving upward to caudal peduncle. Dorsal head profile straight between snout tip and interorbital, making 36–41° angle with body axis and often interrupted by slight bulge at tip of premaxillary pedicel, then rounding to dorsal fin origin; eye small (mean 26.6% HL), smaller than depth preorbital and

positioned in anterior half of head with posterior orbit margin laying on vertical median of head. Long snout with wide, isognathous jaws; teeth on lower jaw in 2–4 rows with anteriormost of outer row large, unequally bicuspid and remaining (lateral) teeth unicuspid; inner row teeth small, unequally tricuspid tending to unicuspid in larger individuals; wide gap between outer row and inner rows. Teeth of lower pharyngeal bone well spaced with sharp cusp; teeth of posterior row enlarged. Lips thickened and concealing most of oral teeth with only larger tips of outer row teeth visible, when mouth opened.



FIGURE 4. Melanochromis kaskazini, holotype, PSU 4546, 121.5 mm SL, male; Manda, Lake Malaŵi, Tanzania.

Dorsal fin with XVI–XVIII (mode XVII) spines and 8–10 (mode 9) soft rays. Anal fin with III spines and 7 or 8 (mode 8) soft rays. First 6–8 dorsal spines gradually increasing in length posteriorly with first spine less than 1/3 length of eighth spine; last 10 spines slightly increasing in length posteriorly with last spine longest; soft dorsal with rounded or subacuminate tip, fourth or fifth ray longest, not or about reaching base of caudal fin. Anal spines progressively increasing in length posteriorly; fifth ray longest, not reaching base of caudal fin. Caudal fin subtruncate to emarginate. Pelvic fin not reaching anal fin in females; reaching first anal spine in males. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base of 10th or 11th dorsal spine.

Flank scales large, ctenoid; abrupt difference to small scales on breast and belly; cheek with 2–7 (mean 4) rows of small scales. Upper branch of lateral line with 20–24 pored scales; lower branch 9–11. Small scales on proximal margin of dorsal fin and on proximal half of caudal fin.

Coloration. Breeding males: head and body cyan blue. Dorsal fin cyan blue with pale blue distal margin and white lappets. Caudal fin cyan blue with pale blue submarginal band and narrow yellow distal margin. Anal fin gray/blue with light blue distal margin and 3–5 small yellow ocelli. Pelvic fins gray/blue with white/light blue leading margin. Pectoral fins with light-gray rays and clear membranes. When in full breeding color, males with blue color, which conceals broad black stripes of subordinate males.

Females: head cream white with blue highlights and two black interorbital bands on snout; gular region off-white. Body cream white with blue highlights and broad (2 full scales) black mid-lateral and dorso-lateral stripes; upper flank scales with light-blue margins; belly and breast off-white. Dorsal fin gray/white with narrow black submarginal band and white lappets with yellow tips; proximal black band on dorsal-fin base continuous with dorso-lateral stripe. Caudal fin bluish white with black spot at base, broad submarginal black band and yellow/orange margin. Anal fin gray proximally and orange/yellow distally. Pelvic fins clear/gray with yellow suffusion distally and with white leading margin and gray submarginal band. Pectoral fins with gray/yellow rays and clear membranes.

TABLE 2. Morphometric and meristic values of *Melanochromis kaskazini* from Manda (holotype and 13 paratypes), Ngwazi (n=5), Makonde (n=1), and Lundu (n=1) in Tanzania. The range includes the holotype.

Melanochromis kaskazini	holotype	mean	range
Standard length, mm	121.5	82.8	53.5–121.5
Head length, mm	40.8	28.9	18.8-40.8
Percent standard length			
Head length	33.6	34.9	33.6–37.8
Body depth	37.5	31.2	26.4–37.5
Snout to dorsal	34.7	35.3	32.5–37.7
Snout to pelvic	38.0	38.6	33.9–43.6
Dorsal base length	58.6	56.3	54.0-58.6
Anterior dorsal to anterior anal	50.8	46.4	42.9-50.8
Anterior dorsal to posterior anal	61.4	58.5	55.9-61.4
Posterior dorsal to anterior anal	30.0	28.2	25.8-30.1
Posterior dorsal to posterior anal	15.7	14.2	13.1–15.7
Posterior dorsal to ventral caudal	20.1	18.5	16.0-20.1
Posterior anal to dorsal caudal	21.1	20.1	18.1–22.4
Anterior dorsal to pelvic–fin origin	34.8	30.2	26.4–34.8
Posterior dorsal to pelvic-fin origin	57.5	55.0	52.3-57.5
Caudal peduncle length	13.1	13.7	12.0-15.4
Least caudal peduncle depth	12.6	11.3	9.8-12.6
Pectoral fin length	22.6	23.2	21.5–25.0
Pelvic fin length	31.9	27.4	22.4–31.9
Percent head length	holotype		
Snout length	37.2	33.8	30.8–37.2
Postorbital head length	44.5	42.4	38.4-44.6
Horizontal eye diameter	23.8	26.6	21.9–32.0
Vertical eye diameter	24.5	25.0	21.3-29.4
Head depth	96.4	79.8	65.3–96.4
Preorbital depth	22.0	21.9	19.3–26.9
Cheek depth	27.7	23.8	19.8–28.0
Lower jaw length	44.6	40.3	36.4–44.6
Interorbital width	22.3	19.6	16.4–22.3
Premaxillary length	25.5	26.8	24.3–34.2
Meristics		mode	range
Dorsal fin spines	17	17	16–18
Dorsal fin rays	9	9	8–10
Anal fin spines	3	3	3
Anal fin rays	8	8	7–8
Pectoral fin rays	13	13	13–14
Pelvic fin rays	5	5	5
Caudal fin rays	17	17	16–18

TABLE 2. (continued)

Melanochromis kaskazini	holotype	mean	range
Lateral line scales	33	33	32–34
Pored scales post lateral line	4	3	2–4
Scale row cheek	4	4	2–7
Gillrakers 1st ceratobranchial	10	10	8–11
Gillrakers 1st epibranchial	3	3	2–4
Teeth outer left lower jaw	12	11	10–16
Teeth row upper jaw	5	4	2–5
Teeth rows lower jaw	3	3	2–4

Field observations. *Melanochromis kaskazini* wanders through the intermediate habitat hunting larger invertebrates and small fishes. At most localities, generally solitary individuals are encountered, but at Makonde and Manda small foraging groups are frequently seen, in particular when SCUBA divers stir debris to which the predators are attracted. Most foraging groups consist of several males in varying degree of sexual maturity with usually a single large male in full blue color. Territorial or courting males have not been observed. *Melanochromis kaskazini* is most often seen at depths varying between 5–40 m.

Distribution. *Melanochromis kaskazini* was encountered along the northeastern shore between Nkanda (9° 33.352' S, 34° 6.479' E) and Lundu (10° 42.535' S, 34° 39.002' E) (Fig. 1). Lundu appears to be the southernmost margin in the distribution of other species as well. We found no apparent barrier in the northernmost part of its distribution that would explain why it was not found north of Nkanda. Another predatory species of *Melanochromis*, an undescribed form referred to as *Melanochromis* 'blue' by Ribbink *et al.* (1983), occurs north of Nkanda. The population density of *M. kaskazini* is higher at Makonde and Manda than at other known localities.

Etymology. The specific epithet *kaskazini* means "northern" in Kiswahili, the language spoken along the shores of the species' distribution.

Melanochromis wochepa new species

(Figs. 5, 7b; Table 3)

Melanochromis dialeptos (part) Konings 2001

Holotype. PSU 4553, 62.5 mm SL, male; Mozambique, Lake Malaŵi, Lumessi, 13° 8.229' S, 34° 47.848' E, Stauffer and Konings, 14 Feb 2002.

Paratypes. PSU 4551, 17, 41.7–65.1 mm SL, data as for holotype; AMNH 246006, 2, 58.6–62.0 mm SL, data as for holotype.

Diagnosis. Melanochromis wochepa is distinguished from its congeners, except M. auratus, M. dialeptos, and M. mossambiquensis, by a steeper-angled vomer (72–80° vs. 35–53°). It is distinguished from M. auratus, M. dialeptos, and M. mossambiquensis by the male coloration pattern which is blue without white stripes and which is brown/black with yellow and pale-blue stripes in males of the other species. Female M. wochepa are distinguished from M. auratus by a submarginal dorsal band that is wider than the mid-lateral and the dorso-lateral stripe. The abdominal yellow stripes in female M. wochepa are thin and never cover the entire lower abdomen, while those in female M. auratus usually cover the entire lower half of the body. M. wochepa is further distinguished from M. dialeptos by a longer head (30.2–33.3 vs. 29.8–31.4 % SL), a deeper body (30.2–34.7 vs. 26.8–31.8 % SL), by a larger distance between the posterior dorsal and pelvic fin (53.3–59.8 % vs. 49.8–55.8 % SL), by a longer pectoral fin (22.8–33.0 % vs. 19.5–24.3 % SL), and by more dorsal-fin rays

(7–10 (mode 9) vs. 7–9 (mode 7)). It is further distinguished from *M. mossambiquensis* by a deeper body as expressed in a larger distance between the origins of the dorsal and anal fins (49.6–54.5 % vs. 47.1–50.8 % SL) and a larger distance between the origins of the dorsal and pelvic fins (30.1–36.4 % vs. 27.6–33.4 % SL), and by a shorter lower jaw (26.7–32.5 % vs. 29.0–41.5 % HL).



FIGURE 5. Melanochromis wochepa, holotype, PSU 4553, 62.5 mm SL, male; Lumessi, Lake Malaŵi, Mozambique.

Description. Morphometric ratios and meristic values appear in Table 3. Small, oblong species (mean BD 33.2% SL) with greatest body depth at about base of third dorsal spine. Dorsal body profile gradually curving downward to caudal peduncle; ventral body profile slightly convex between pelvic fins and vent then tapering upward along base anal fin to caudal peduncle. Dorsal head profile rounded, curving almost continuously between snout tip and dorsal fin origin; eye (mean 33.9% HL) larger than depth preorbital and positioned entirely in anterior half of head; steep, rounded snout and slightly retrognathous jaws; wide tooth bands with 6–9 rows in lower and upper jaws with teeth in outer rows bicuspid and teeth in inner rows tricuspid.

Dorsal fin with XVII–XIX (mode XVIII) spines and 7–10 (mode 9) soft rays. Anal fin with III spines and 7 or 8 (mode 7) soft rays. First 3 or 4 dorsal spines gradually increasing in length posteriorly with first spine less than ½ length of fourth spine; last 14 spines slightly increasing in length posteriorly with last spine longest; soft dorsal with rounded (females) or subacuminate (males) tip, third or fourth ray longest, not reaching in females and about reaching base of caudal fin in males. Anal spines progressively increasing in length posteriorly; third or fourth ray longest, not reaching (in females) or just reaching (males) base of caudal fin. Caudal fin subtruncate to emarginate. Pelvic fin not reaching anal fin in females; reaching first anal spine in males. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base 10th or 11th dorsal spine.

Flank scales large, ctenoid; abrupt difference to small scales on breast; cheek with 4–7 (mean 5) rows of small scales. Upper branch of lateral line with 22–27 pored scales; lower branch 9–13. Small scales on proximal posterior margins of dorsal and anal fins and on proximal half of caudal fin.

Coloration. Breeding males: head blue; snout gray/blue with two dark-gray/blue interorbital bands; post-orbital head with few white/golden spots behind eye. Body blue with sometimes faint midlateral pale blue stripe; caudal peduncle blue; belly and breast blue/gray-blue. Dorsal fin gray/blue with white/light blue margin and yellow lappets. Caudal fin blue with pale-blue rays and yellow distal membranes. Anal fin blue with black submarginal band and light-blue distal margin; 1–3 yellow ocelli in trailing part. Pelvic fins black/dark-blue with light-blue leading margin. Pectoral fins with gray rays and clear membranes.

Females: head gray/yellow with gray/white gular region and irregular yellow markings, snout with two black interorbital bands. Body gray/white with narrow black midlateral and dorso-lateral stripes, irregular

TABLE 3. Morphometric and meristic values of *Melanochromis wochepa* from Lumessi, Mozambique (holotype and 19 paratypes). The range includes the holotype.

Melanochromis wochepa	holotype	mean	range
Standard length, mm	62.5	57.0	41.7–65.1
Head length, mm	19.7	18.0	12.6-20.1
Percent standard length			
Head length	31.5	31.5	30.2-33.3
Body depth	34.7	33.2	30.2-34.7
Snout to dorsal	36.0	35.2	32.7–37.7
Snout to pelvic	32.3	34.6	27.8-38.0
Dorsal base length	62.7	59.7	56.5-62.7
Anterior dorsal to anterior anal	52.8	52.2	49.6–54.5
Anterior dorsal to posterior anal	66.0	63.5	60.3-66.4
Posterior dorsal to anterior anal	30.8	29.1	27.0-31.2
Posterior dorsal to posterior anal	16.4	15.2	13.8-16.4
Posterior dorsal to ventral caudal	17.8	16.9	16.0-18.0
Posterior anal to dorsal caudal	18.5	19.1	17.8-20.0
Anterior dorsal to pelvic-fin origin	34.9	34.0	30.1–36.4
Posterior dorsal to pelvic-fin origin	58.0	56.5	53.3-59.8
Caudal peduncle length	12.7	13.3	11.7–15.3
Least caudal peduncle depth	10.6	10.3	8.3-11.3
Pectoral fin length	27.0	27.6	22.8-33.0
Pelvic fin length	23.9	23.8	21.0-27.1
Percent head length	holotype		
Snout length	37.7	34.7	26.7–38.3
Postorbital head length	43.3	43.7	41.1–48.0
Horizontal eye diameter	31.2	33.9	31.2-37.9
Vertical eye diameter	31.4	34.8	31.4–39.6
Head depth	106.5	97.1	87.2-106.5
Preorbital depth	15.7	16.2	11.7–20.0
Cheek depth	25.2	25.0	20.4–28.2
Lower jaw length	26.7	29.3	26.7–32.5
Interorbital width	23.5	24.2	21.9–27.3
Premaxillary length	25.2	24.0	19.8–26.8
Meristics		mode	range
Dorsal fin spines	18	18	17–19
Dorsal fin rays	9	9	7–10
Anal fin spines	3	3	3
Anal fin rays	7	7	7–8
Pectoral fin rays	14	14	13–14
Pelvic fin rays	6	6	6
Caudal fin rays	17	17	16–18
Lateral line scales	32	32	30–33

TABLE 3. (continued)

Melanochromis wochepa	holotype	mean	range
Pored scales post lateral line	3	3	2–5
Scale row cheek	5	5	4–7
Gillrakers 1st ceratobranchial	9	9	9–11
Gillrakers 1st epibranchial	2	3	1–3
Teeth outer left lower jaw	15	15	14–17
Teeth row upper jaw	6	7	5–9
Teeth rows lower jaw	6	7	6–9

orange/yellow stripe between these two stripes; gray/brown irregular band along base dorsal fin. Dorsal fin white/light-yellow with broad black submarginal band and yellow lappets, gray/brown irregular band proximally. Caudal fin with irregular pattern of yellow, black, and pale-blue markings throughout. Anal fin white/pale-blue with yellow distal margin and black pigment on anterior part; 1 or 2 yellow ocelli in trailing part. Pelvic fins yellow with black markings, narrow white leading margin. Pectoral fins clear with gray rays.

Distribution. *Melanochromis wochepa* is restricted to the eastern shoreline between Nkhungu Point (12° 58.849' S, 34° 45.814' E) and the Lumessi River (13° 8.987' S, 34° 47.893' E) in Mozambique (Fig. 1).

Field observations. Habitat preference and behavior of *M. wochepa* is similar to those of *M. auratus* and *M. dialeptos*. It occurs in the shallow rocky habitat and is mostly seen solitary, although it is not an uncommon appearance. Males in breeding coloration do not defend a territory, but displays between males are frequent but of short duration. *Melanochromis wochepa* primarily feeds from the aufwuchs on rocks from which it picks algal strands and diatoms.

Etymology. The specific epithet, a noun in apposition, is derived from Chinyanja, the local language around the lake, and means "small" referring to the small adult size of this species.

Melanochromis mossambiquensis new species (Figs. 6, 7c; Table 4)

Melanochromis sp. "auratus elongate" Konings 1995

Holotype. PSU 4555, 76.1 mm SL, male; Mozambique, Lake Malaŵi, Minos Reef, 12° 53.213' S, 34° 45.013' E, Stauffer and Konings, 15 Feb 2002.

Paratypes. PSU 4552, 17, 49.4–74.9 mm SL, data as for holotype; AMNH 246008, 2, 50.8–63.4 mm SL, data as for holotype.

Diagnosis. *Melanochromis mossambiquensis* is distinguished from its congeners, except *M. auratus*, *M. dialeptos*, and *M. wochepa*, by a steeper-angled vomer (72–80° vs. 35–53°). It is distinguished from *M. auratus* by a mid-lateral and a dorso-lateral black stripe that is narrower than the submarginal black band in the dorsal fin, while in *M. auratus* the submarginal dorsal stripe is narrower than those on the flank. The abdominal yellow stripes in *M. mossambiquensis* are thin and never cover the entire lower abdomen as they do in *M. auratus*. The lower lobe of the caudal fin contains black spots while that of female *M. auratus* is yellow without black markings. Male *M. mossambiquensis* are distinguished from those of *M. auratus* by the lack of a narrow, yellow mid-lateral stripe. Male *M. mossambiquensis* are distinguished from those of *M. wochepa* by a brown/black body with white dorso-lateral and mid-lateral stripes while that of male *M. wochepa* is blue without stripes. *M. mossambiquensis* is distinguished from *M. wochepa* by a shallower body as expressed in a shorter distance between the origins of the dorsal and anal fin (47.1–50.8 % vs. 49.6–54.5 % SL) and a shorter distance between the origins of the dorsal and pelvic fins (27.6–33.4 % vs. 30.1–36.4 % SL), and by a longer lower jaw (29.0–41.5 % vs. 26.7–32.5 % HL). It is distinguished from *M. dialeptos* by a more

elongate body as expressed in a larger distance between the posterior dorsal and the pelvic fin origin (52.9–60.7 % vs. 49.8–55.8 % SL), a longer snout (29.2–40.3 % vs. 25.9–35.2 % HL), and by fewer rows of scales on the cheek (3 or 4 vs. 4–7).

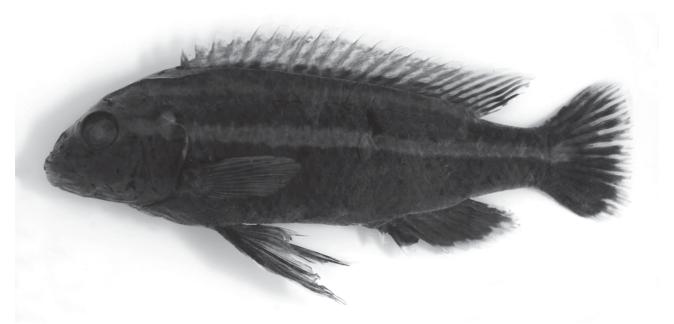


FIGURE 6. *Melanochromis mossambiquensis*, holotype, PSU 4555, 76.1 mm SL, male; Minos Reef, Lake Malaŵi, Mozambique.

Description. Morphometric ratios and meristic values appear in Table 4. Small, somewhat elongate species (mean BD 30.9% SL) with greatest body depth at base of third or fourth dorsal spine. Dorsal body profile gradually curving downward to caudal peduncle; ventral body profile increasingly tapering upward to caudal peduncle. Dorsal head profile rounded, curving almost continuously between snout tip and dorsal fin origin; eye (mean 32.1% HL) larger than depth preorbital and positioned entirely in anterior half of head; moderately steep, rounded snout and slightly retrognathous jaws; teeth on lower and upper jaws in 3–6 rows, with those of outer rows bicuspid and those of inner rows tricuspid. Teeth of lower pharyngeal bone tightly packed with none enlarged or rounded. Vomer in single specimen (Nkhungu Reef) at 72° with parasphenoid.

Dorsal fin with XVII–XIX (mode XVIII) spines and 7–9 (mode 8) soft rays. Anal fin with III spines and 6–8 (mode 7) soft rays. First 4–6 dorsal spines gradually increasing in length posteriorly with first spine less than ½ length of sixth spine; last 12 spines slightly increasing in length posteriorly with last spine longest; soft dorsal with rounded tip, fourth ray longest, not or about reaching base of caudal fin. Anal spines progressively increasing in length posteriorly; fourth or fifth ray longest, not reaching base of caudal fin. Caudal fin subtruncate to emarginate. Pelvic fin not reaching anal fin. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base of 10th or 11th dorsal spine.

Flank scales large, ctenoid; abrupt difference to fine scales on breast; cheek with 3 or 4 (mean 3) rows of small scales. Upper branch of lateral line with 21–28 pored scales; lower branch 8–14. Small scales on proximal posterior margins of dorsal and anal fins and on proximal half of caudal fin.

Coloration. Breeding males: head dark blue/black; snout dark blue/gray with some individuals with pale-blue interorbital band; post-orbital head with pale blue horizontal band behind eye to edge of gill cover. Body dark blue/black with dorso-lateral and midlateral pale blue stripes; area above dorso-lateral stripe dark blue/black with light-blue highlights; caudal peduncle dark blue/black with pale blue midlateral stripe, upper part with pale blue highlights; belly and breast dark blue/black. Dorsal fin light blue with dark blue/black proximal band and yellow distal margin, wider in trailing part. Caudal fin dark blue/black with pale-blue rays and yellow distal margin. Anal fin black, with 1 or 2 orange/yellow ocelli and pale blue ventral border. Pelvic fins black with white/light-blue leading margin. Pectoral fins with dark gray rays and clear membranes.

TABLE 4. Morphometric and meristic values of *Melanochromis mossambiquensis* from Minos Reef, Mozambique (holotype and 19 paratypes). The range includes the holotype.

Melanochromis mossambiquensis	holotype	mean	range
Standard length, mm	76.1	61.8	49.4–76.1
Head length, mm	22.5	19.3	15.4–23.1
Percent standard length			
Head length	29.5	31.3	29.5–33.2
Body depth	30.7	30.9	29.1–33.6
Snout to dorsal	33.1	34.5	32.9–36.6
Snout to pelvic	35.1	35.9	33.0–39.2
Dorsal base length	60.3	58.5	54.3-60.4
Anterior dorsal to anterior anal	48.9	48.9	47.1–50.8
Anterior dorsal to posterior anal	62.7	61.3	58.7-62.9
Posterior dorsal to anterior anal	29.0	28.5	26.2–30.0
Posterior dorsal to posterior anal	15.0	14.7	13.4–16.8
Posterior dorsal to ventral caudal	19.3	17.1	15.1–19.3
Posterior anal to dorsal caudal	22.5	20.0	18.0-22.5
Anterior dorsal to pelvic-fin origin	32.6	30.5	27.6–33.4
Posterior dorsal to pelvic-fin origin	56.8	56.3	52.9-60.7
Caudal peduncle length	15.4	14.1	12.5–15.4
Least caudal peduncle depth	10.9	10.5	9.5–11.5
Pectoral fin length	20.7	22.1	20.4–23.8
Pelvic fin length	31.4	26.5	23.8–32.9
Percent head length	holotype		
Snout length	34.7	32.3	29.2–40.3
Postorbital head length	45.8	43.7	42.1–45.8
Horizontal eye diameter	30.1	32.1	29.5–36.1
Vertical eye diameter	30.1	31.6	28.6–34.8
Head depth	96.7	88.2	77.2–101.4
Preorbital depth	19.0	18.2	15.3–20.5
Cheek depth	25.2	26.3	22.2–32.0
Lower jaw length	33.2	32.8	29.0–41.5
Interorbital width	25.3	22.1	18.6–25.3
Premaxillary length	24.0	25.6	22.6–27.5
Meristics		mode	range
Dorsal fin spines	18	18	17–19
Dorsal fin rays	8	8	7–9
Anal fin spines	3	3	3
Anal fin rays	7	7	6–8
Pectoral fin rays	11	13	11–15
Pelvic fin rays	6	6	5–6
Caudal fin rays	16	16/17	16–17
Lateral line scales	33	32	31–34

TABLE 4. (continued)

Melanochromis mossambiquensis	holotype	mean	range
Pored scales post lateral line	4	4	3–4
Scale row cheek	3	3	3–4
Gillrakers 1st ceratobranchial	11	10	8–11
Gillrakers 1st epibranchial	2	3	2–4
Teeth outer left lower jaw	17	16	11–17
Teeth row upper jaw	6	6	3–6
Teeth rows lower jaw	6	6	3–6

Females: head gray/yellow with gray/white gular region and irregular orange/yellow markings, snout with two black interorbital bands. Body gray/white with narrow black midlateral and dorso-lateral stripes, irregular orange/yellow stripe between two stripes; gray/brown irregular band below base of dorsal fin; 2–4 irregular yellow stripes on abdomen. Gray-yellow dorsal fin with broad black submarginal band bordered with narrow white stripes, yellow lappets and few black spots in trailing portion. Caudal fin clear with many yellow, black, and pale-blue markings throughout; lower lobe with yellow margin. Anal fin yellow with pale blue proximal band and black pigment on anterior part. Pelvic fins yellow with narrow white leading margin and, in some individuals, indistinct gray band anteriorly. Pectoral fins clear.

Distribution. *Melanochromis mossambiquensis* occurs between Chuanga (12° 38.278' S, 34° 47.264' E) and Nkhungu Reef (12° 57.434' S, 34° 45.498' E) in Mozambique (Fig. 1). The populations observed—but not collected—at Metangula and N'kolongwe (Fig. 1) appear to consist of individuals with longer snouts and shallower bodies.

Field observations. *Melanochromis mossambiquensis* is very common at Minos Reef (type locality) and often gathers in foraging groups feeding from the aufwuchs of the small rocks of the intermediate (sand-rock interface) habitat. Males in breeding coloration are normally solitary and rarely join the foraging groups. Territoriality is rare, but quarrels between males in breeding coloration are common and mainly consist of chasing a competitor from the feeding site.

Etymology. The specific epithet refers to the species' restricted distribution along the Mozambique shore of the lake.

Discussion

Tawil (2002) gives an expanded diagnosis of *Melanochromis* for which we propose some adjustments. His first diagnostic character refers to the most important distinction between *Melanochromis* and other mbuna genera: a contrasting juvenile coloration consisting of 2 or 3 black horizontal bands on a light background, the bands can sometimes be fragmented. The lower band is always midlateral, and the dorso-lateral band(s) are sometimes absent or located near the dorsal fin. In our observations of wild individuals the midlateral band is never fragmented in juveniles, and the posterior half of the band may become fragmented in females of *M. brevis* only. Therefore we propose to enhance the first and most important diagnostic character of *Melanochromis* as follows: a basic melanin pattern which consists of two black horizontal lateral stripes on a light background; the mid-lateral stripe, which is always solid in appearance, straddles the lower arm of the lateral-line system, and the dorso-lateral stripe, which can be fragmented, lies between the dorsal-fin base and the mid-lateral stripe. The solid, mid-lateral stripe is often wider, approximately 2–3 scales, than the dorso-lateral one which is 1–2 scales wide.

The second diagnostic character refers to the reversal in color pattern in breeding males: in many species there is a redistribution of the melanic areas (reversal) in dominant individuals (males and, perhaps, old females) (Tawil 2002). In the type species and in 11 other species, the basic pattern, always visible in juveniles

and females, becomes reversed in adult males, i.e. the entire body of the breeding male first becomes (very) dark—blue, brown, or black—and, secondly, in the position of the two black stripes there are then two light-



FIGURE 7. a. A non-territorial male *Melanochromis kaskazini* (approx. 105 mm SL) at Ngwazi, Lake Malaŵi, Tanzania; inset: a female (approx. 65 mm SL) at Nkanda, Lake Malaŵi, Tanzania; b. two males of *Melanochromis wochepa* (approx. 60 mm SL) at Lumessi, Mozambique; inset: a female (approx. 50 mm SL) at same location; c. a male *Melanochromis mossambiquensis* (approx. 70 mm SL) at Minos Reef, Mozambique; inset: a female (approx. 55 mm SL) at same location.

colored solid stripes—white, yellow, or blue. This sex-related reversed pigmentation pattern is unique among Malaŵi cichlids. In three species, *M. lepidiadaptes, M. wochepa*, and in *M. kaskazini*, this reversal is incomplete. The basic melanin pattern is present in females and juveniles, but in the male breeding coloration, which is entirely sky-blue for all three species, the background color becomes darker (sky-blue), and the black stripes disappear, although these are not converted to a lighter, contrasting color.

Tawil's (2002) other diagnostic characters include an elongate, sub-cylindrical morphology, a long snout, and a large mouth suggesting a predatory life style; weak territoriality but with a high intraspecific intolerance; propensity of protracted retention of fry in the mouth, longer than that is the case with members of *Pseudotropheus*. The latter two characteristics are useful distinguishing attributes when working with live individuals, but we want to remove a predatory morphology from the diagnosis as several members, *M. auratus, M. dialeptos, M. wochepa*, and *M. mossambiquensis*, have neither sub-cylindrical morphologies nor predatory propensities.

The main characteristic that delimits *M. melanopterus* from *M. heterochromis* is the length of the lower jaw in relation to head length, which is 37.2–41.7 % HL in *M. melanopterus* (Thumbi East; n=20) and 29.3–34.6 % HL in *M. heterochromis* (Thumbi East; n=20). The single type specimen of *M. mellitus* (Fig. 2d) has a lower jaw length of 39.4 % HL and thus falls within the range of *M. melanopterus*. It is reportedly from Mumbo Island and lacks any horizontal stripes on the flank in the preserved state, which is common for preserved females of *M. melanopterus*. Its live coloration was reported as yellow with stripes (Johnson 1976), and such individuals have been observed at Mumbo Island (mistaken for *M. vermivorus* in Konings 2001). Those individuals, however, were very slender, and we are now convinced that they represent young males of *M. melanopterus* in the process of acquiring the breeding coloration. The body depth of the type of *M. mellitus* is 27.8 % SL which falls in the range of *M. melanopterus* (Thumbi East Island (n=20): 27.1–32.0 % SL) rather than in that of *M. heterochromis* (Thumbi East Island (n=20): 31.9–36.1 % SL). These three key characters of *M. mellitus*, in our opinion, demonstrate that it is conspecific with *M. melanopterus*, and thus *M. mellitus* is a junior synonym.

Without much doubt it can be said that *M. melanopterus* and *M. vermivorus* are closely related species, and at some point one could even argue that these two are mere geographical variants of a single species. Observing these two forms in the field, however, supports the premise that they are heterospecific. The difference in habitat preference is most pronounced in their depth distributions: *M. melanopterus* at Thumbi East Island occurs at a much deeper part of the rocky habitat (highest population density usually at about 20 m) than *M. vermivorus* at Nkhudzi or at Boadzulu Island (highest density shallower than 10 m). It is probable that the presence of *M. heterochromis* has influenced the habitat preference of *M. melanopterus* at Thumbi East Island, because the former species is normally found in very shallow water, and its depth distribution hardly overlaps with that of *M. melanopterus*. *Melanochromis heterochromis* is primarily an herbivorous species while *M. melanopterus* is a predatory mbuna (it also has much larger jaws). On the other hand, *M. vermivorus* does not share its habitat with *M. heterochromis* and may thus suffer less competition foraging in the richer upper regions of the rocky habitat and/or employ a wider spectrum of feeding strategies. For these reasons we believe it sensible to regard these two taxa as heterospecific.

Along the Mozambique shore of the lake, a similar situation is found among *M. mossambiquensis* and *M. dialeptos*; the morphological differences between these two taxa could as well be attributed to geographical variation within a single species—albeit with a disjunct distribution. The feeding behavior and habitat preference of *M. dialeptos* is much closer to *M. wochepa* as it is restricted to the shallow rocky habitat and appears to feed almost exclusively on aufwuchs, while *M. mossambiquensis* occurs over a much larger depth distribution and employs a wider feeding spectrum. Also here, we believe that the habitat preference and feeding regime of *M. dialeptos* and *M. wochepa* are influenced by the presence of *M. simulans*, another, seemingly closely-related (based on coloration) and predatory member of the genus. The latter is sympatric with *M. dialeptos* and *M. wochepa*—albeit at a much deeper level of the habitat—but which is not found within the distribution of *M. mossambiquensis*. For these reasons we regard *M. mossambiquensis* heterospecific from *M. dialeptos*.

TABLE 5. Nomenclatural events in the genus *Melanochromis*.

Species in <i>Melanochromis</i> Author(s)	Suggested Reclassification Author(s)	Currently Residing in Melanochromis
Melanochromis melanopterus Trewavas 1935		Melanochromis melanopterus
Melanochromis vermivorus Trewavas 1935		Melanochromis vermivorus
<i>Melanochromis brevis</i> Trewavas 1935	Pseudotropheus brevis by Johnson 1975	Melanochromis brevis
Melanochromis perspicax Trewavas 1935	Pseudotropheus perspicax by Loiselle 1979 and Ribbink et al. 1983	
<i>Melanochromis labrosus</i> Trewavas 1935	Haplochromis labrosus by Burgess 1976	Melanochromis labrosus
<i>Pseudotropheus auratus</i> Boulenger 1897	Melanochromis auratus by Burgess 1976	Melanochromis auratus
Pseudotropheus johannii Eccles 1973	Melanochromis johannii by Burgess 1976 Pseudotropheus johannii by Tawil 2002	
Melanochromis simulans Eccles 1973		Melanochromis simulans
<i>Melanochromis exasperatus</i> Burgess 1976	Pseudotropheus joanjohnsonae by Stock 1976	
Labidochromis joanjohnsonae Johnson 1974	Pseudotropheus joanjohnsonae by Stock 1976 Melanochromis joanjohnsonae by Lewis 1980	Melanochromis joanjohnsonae
Melanochromis parallelus Burgess and Axelrod 1976	Melanochromis chipokae by Schraml 1998	Melanochromis parallelus
<i>Melanochromis chipokae</i> Johnson 1975		Melanochromis chipokae
<i>Melanochromis loriae</i> Johnson 1975	Melanochromis chipokae by Konings 2001	Melanochromis loriae
<i>Melanochromis interruptus</i> Johnson 1975	Pseudotropheus interruptus by Tawil 2002	
Melanochromis mellitus Johnson 1976	Melanochromis vermivorus by Schraml 1998 and Konings 2001 Melanochromis melanopterus this paper	
<i>Melanochromis robustus</i> Johnson 1985		Melanochromis robustus
<i>Melanochromis crabro</i> Ribbink and Lewis 1982	Pseudotropheus crabro by Trewavas 1984	
Melanochromis heterochromis Bowers and Stauffer 1993	Melanochromis vermivorus by Konings 1995 and Schraml 1998	Melanochromis heterochromis
<i>Melanochromis dialeptos</i> Bowers and Stauffer 1997		Melanochromis dialeptos

TABLE 5. (continued)

Species in Melanochromis	Suggested Reclassification	Currently Residing in Melanochromis
Author(s)	Author(s)	
Melanochromis cyaneorhabdos	Pseudotropheus cyaneorhabdos	
Bowers and Stauffer 1997	by Tawil 2002	
Melanochromis perileucos	Pseudotropheus perileucos	
Bowers and Stauffer 1997	by Tawil 2002	
Melanochromis baliodigma		Melanochromis baliodigma
Bowers and Stauffer 1997		
Melanochromis xanthodigma	Melanochromis baliodigma	
Bowers and Stauffer 1997	by Konings 2001 and Tawil 2002	
Melanochromis lepidiadaptes Bowers and Stauffer 1997		Melanochromis lepidiadaptes
Melanochromis elastodema	Melanochromis interruptus	
Bowers and Stauffer 1997	by Schraml 1998 and Konings 2001	
Melanochromis benetos	Melanochromis robustus	
Bowers and Stauffer 1997	by Konings 2001	
	Pseudotropheus benetos	
	this paper	
Melanochromis kaskazini		Melanochromis kaskazini
Konings-Dudin, Konings and		
Stauffer		
Melanochromis wochepa		Melanochromis wochepa
Konings-Dudin, Konings and		
Stauffer		
$Me la no chromis\ moss ambiquens is$		Melanochromis mossambiquensis
Konings-Dudin, Konings and		
Stauffer		

In our evaluation of the relationship between *M. kaskazini* and already described predatory species in *Melanochromis*, we discovered that the form previously described as *Melanochromis benetos* Bowers and Stauffer 1997 is congruent with a herbivorous species that has been referred to as *Pseudotropheus* sp. 'tursiops chitande' (Konings 2001). Although females of this species exhibit two longitudinal stripes on the flank, the nature of these stripes—rows of small spots—is incompatible with the diagnosis of *Melanochromis*. Although its long snout might indicate a more predacious regime and thus resemble the predatory members of *Melanochromis*, *Pseudotropheus benetos* is an algae browser, which is mostly found in the upper rocky habitat in the northern part of the lake.

The initial distinction between *Melanochromis* and *Pseudotropheus* relating to the size and configuration of the pharyngeal teeth (Trewavas 1935) is no longer considered a diagnostic feature—in fact, no distinction could be found between the pharyngeal jaws of the type species of either genus (Trewavas 1984). Another characteristic, relating to the arrangement of the oral teeth in U-shaped bands and extended on each side by a single row of unicuspid teeth (Trewavas 1984), is shared with many members of *Pseudotropheus* and has thus no diagnostic value. It was stated as a characteristic of *Melanochromis* by Trewavas (1984) but never specifically considered as a diagnostic feature. We regard the basic melanin pattern one of the important characteristics in classifying Malaŵi cichlids, and species of *Melanochromis* have a unique pattern that is—incomplete in some—reversed in adult males. Since the inception of the genus many workers have suggested alternative classifications for its members (Table 5), and over time the diagnosis has been enhanced and refined, but, currently, we still regard both *Melanochromis* and *Pseudotropheus* as polyphyletic.

Comparative material examined

Melanochromis auratus: PSU 4549, 20, 53.1–75.4 mm SL; Malaŵi, Lake Malaŵi, Namalenje Island, 13° 43.843' S, 34° 38.466' E, S. M. Grant, 23 Mar. 1995. *Melanochromis dialeptos*: PSU 2649 (types), 10, 43.4–67.4 mm SL; Malaŵi, Lake Malaŵi, Masinje, 13° 35' S, 34° 51'E; Stauffer, Feb. 1992; PSU 1546, 3, 46.1–55.5 mm; Malaŵi, Lake Malaŵi, Masinje, 13° 35' S, 34° 51' E, Bowers and Stauffer, Feb. 1992. *Melanochromis heterochromis*: PSU 4548, 18, 47.4–62.4 mm SL and AMNH 246009, 2, 56.2–59.1; Malaŵi, Lake Malaŵi, Thumbi East Island (Monkey Bay), 14° 3.840' S, 34° 55.261' E, Stauffer and Konings, 10 Oct. 2004. *Melanochromis melanopterus*: PSU 4547, 16, 54.5–76.4 mm SL and AMNH 246005, 2, 58.6–71.6; Malaŵi, Lake Malaŵi, Thumbi East Island, 14° 3.840' S, 34° 55.261' E, Stauffer and Konings, 10 Oct. 2004. Holotype of *M. mellitus*, AMNH 35387, 1, 79.4 mm SL; Malaŵi, Lake Malaŵi, Mumbo Island; Davies, 1976.

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References

- Barel, C.D.N., Van Oijen, M.J.P., Witte, F. & Witte-Maas, E.L.M. (1977) An introduction of the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria. Part A. *Netherlands Journal of Zoology*, 27, 333–389.
- Bookstein, F.L., Chernoff, B., Elder, R., Humphries, J., Smith, G. & Strauss, R. (1985) Morphometrics in evolutionary biology. *Academy of Natural Sciences Philadelphia*, Special Publications, 15, 1–277.
- Bowers, N.J. & Stauffer Jr., J.R. (1993) New species of rock-dwelling cichlid (Pisces: Cichlidae) from Lake Malawi, Africa, with comments on *Melanochromis vermivorus* Trewavas. *Copeia*, 1993, 715–722.
- Bowers, N.J. & Stauffer Jr., J.R. (1997) Eight new species of rock-dwelling cichlids of the genus *Melanochromis* (Teleostei: Cichlidae) from Lake Malawi, Africa. *Ichthyological Explorations of Freshwaters*, 8, 49–70.
- Burgess, W.E. (1976) A new *Melanochromis* from Lake Malawi, with comments on the genus. *Tropical Fish Hobbyist*, 24, 61–65.
- Eccles, D.H. & Trewavas, E. (1989) *Malawian cichlid fishes. The classification of some Haplochromine genera*. Lake Fish Movies, Herten, Germany, 335 pp.
- Genner, M.J. & Turner, G.F. (2005) The mbuna cichlids of Lake Malawi: a model for rapid speciation and adaptive radiation. *Fish and Fisheries*, 6, 1–34.
- Humphries, J.M., Bookstein, F.L., Chernoff, B., Smith, G. R., Elder, R.L. & Poss, S.G. (1981) Multivariate discrimination by shape in relation to size. *Systematic Zoology*, 30, 291–308.
- Johnson, D.S. (1975) More new Malawi cichlids. Today's Aquarist, 2, 15-26.
- Johnson, D.S. (1978) *Mbuna—The colorful rock-dwelling cichlid fishes of Lake Malawi*. Pisces Publishing Corp., Norwalk, Connecticut, 84 pp.
- Konings, A. (1995) *Malaŵi cichlids in their natural habitat*. 2nd ed., Cichlid Press, St Leon-Rot, Germany, 352 pp.
- Konings, A. (2001) Malaŵi cichlids in their natural habitat. 3rd ed., Cichlid Press, El Paso, Texas, 352 pp.
- Leviton, A.E., Gibbs, R.H., Heal, E. & Dawson, C. E. (1985) Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985, 802–832.
- Lewis, D.S.C. (1980) A further examination of the taxonomic status of *Labidochromis joanjohnsonae* Johnson 1974 with a redescription of the species (Pisces Cichlidae). *Revue de Zoologie africaine*, 94, 959–971.
- Loiselle, P.V. (1978) Reflections on the generic placement of *Haplochrowis labrosus*. *Buntbarsche Bulletin* (ACA), 67,16–18.
- Loiselle, P.V. (1979) Melanochromis. The beautiful baddies from Lake Malawi. Freshwater and Marine Aquarium, 2,

17-23.

- Ribbink, A.J. & Lewis, D.S.C. (1982) *Melanochromis crabro* sp. nov.: a cichlid fish from Lake Malawi which feeds on ectoparasites and catfish eggs. *Netherlands Journal of Zoology*, 32, 72–87.
- Ribbink, A.J., Marsh, B.A., Marsh, A.C., Ribbink, A.C. & Sharp, B.J. (1983) A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *South African Journal of Zoology*, 18, 149–310.
- Schraml, E. (1998) African cichlids I (Malawi, mbuna). Aqualog, Mörfelden-Walldorf, Germany, 240 pp.
- Spreinat, A. (1994) Malawisee-Cichliden aus Tansania. Unitext Verlag, Bovenden, Germany, 316 pp.
- Stauffer Jr., J.R. (1991) Description of a facultative cleanerfish (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Copeia*, 1991, 141–147.
- Stauffer Jr., J.R. (1994) A new species of *Iodotropheus* (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Ichthyological Explorations of Freshwaters*, 5, 331–344.
- Stauffer Jr., J. R. & Hert, E. (1992) *Pseudotropheus callainos*, a new species of mbuna (Cichlidae), with analyses of changes associated with two intra-lacustrine transplantations in Lake Malaŵi, Africa. *Ichthyological Explorations of Freshwaters*, 3, 253–264.
- Tawil, P. (2002) Notes sur le genre *Melanochromis* et l'appartenance générique de *Pseudotropheus johannii* Eccles, 1973, et espèces apparentées. *L'an Cichlidé*, 2, 61–68.
- Trewavas, E. (1935) A synopsis of the cichlid fishes of Lake Nyasa. *Annals and Magazine of Natural History*, 10(16), 65–118.
- Trewavas, E. (1984) Nouvel examen des genres et sous-genres du complexe *Pseudotropheus-Melanochromis* du lac Malawi (Pisces, Perciformes, Cichlidae). *Revue française d'Aquariologie*, 10(1983), 97–106.